VOLUME XXXVIII NUMBER 6

BOTANICAL GAZETTE

DECEMBER, 1904

THE VARIATION OF SOME CALIFORNIA PLANTS.

EDWIN BINGHAM COPELAND.

(WITH NINE FIGURES)

I.

ONE of the first features of the flora of the mountainous and rather dry parts of California to impress one familiar with that of the eastern states and the Mississippi valley is the exceeding variability of a great many of the plants. While every botanist going into this field must have been struck by this fact, and some have remarked upon it, as JEPSON well does in the introduction to his *Botany of Middle Western California*, it has never been the subject of any particular study.

The good material for such work is practically unlimited; but my time has not been so, and it has seemed to me that the study of a few plants ought to show what is most characteristic of variation in this region. I have found that the study of these few has given me a plausible explanation of the great local variability, and at the same time has strengthened views already held as to the commonness of variation at other times in the history of plants beside their conception, and as to the generic homogeneity of continuous and discontinuous variation. Out of the material I have worked over, it will suffice for all purposes if I describe the variation of a few woody plants of wide occurrence, and of a few apparently monstrous ferns and the lesser variations connecting them with normal forms. The woody plants selected are several oaks growing near Palo Alto or Chico, and *Rhamnus californica, Arctostaphylos tomentosa, Ceano-*

thus sorediatus, and *Baccharis pilularis*, shrubs of the Palo Alto neighborhood, of frequent occurrence and reasonably independent as to altitude, soil, and exposure. As a further limitation, this account is confined with a single exception to the leaves of these plants; variation in other features—for instance in the scales of the cup of Quercus —is not less conspicuous.

QUERCUS CHRYSOLEPIS Liebmann.

The leaves of oaks are exceedingly variable everywhere, but the differences between the leaves of this species on the same tree, or on neighboring trees, are conspicuous even in such a genus. *Figs. 1–3* are from neighboring trees, growing in the mountains back of Stanford University. Each tree had a well-defined leaf character, as these outlines, each representing leaves of one season's growth on one axis, indicate. The venation of the leaves on each tree was as characteristic as the outline. As a rule, older trees have more entire leaves, but this is not at all constant; all my specimens are from acorn-bearing trees. All the leaves figured grew on well-illuminated parts of the trees. In the three trees furnishing these leaves the variation in leaf-character was an attribute of the entire tree, and must therefore have occurred at a time in the tree's history when it or the stage in its ancestry where the variation occurred was a single cell, or (possibly)

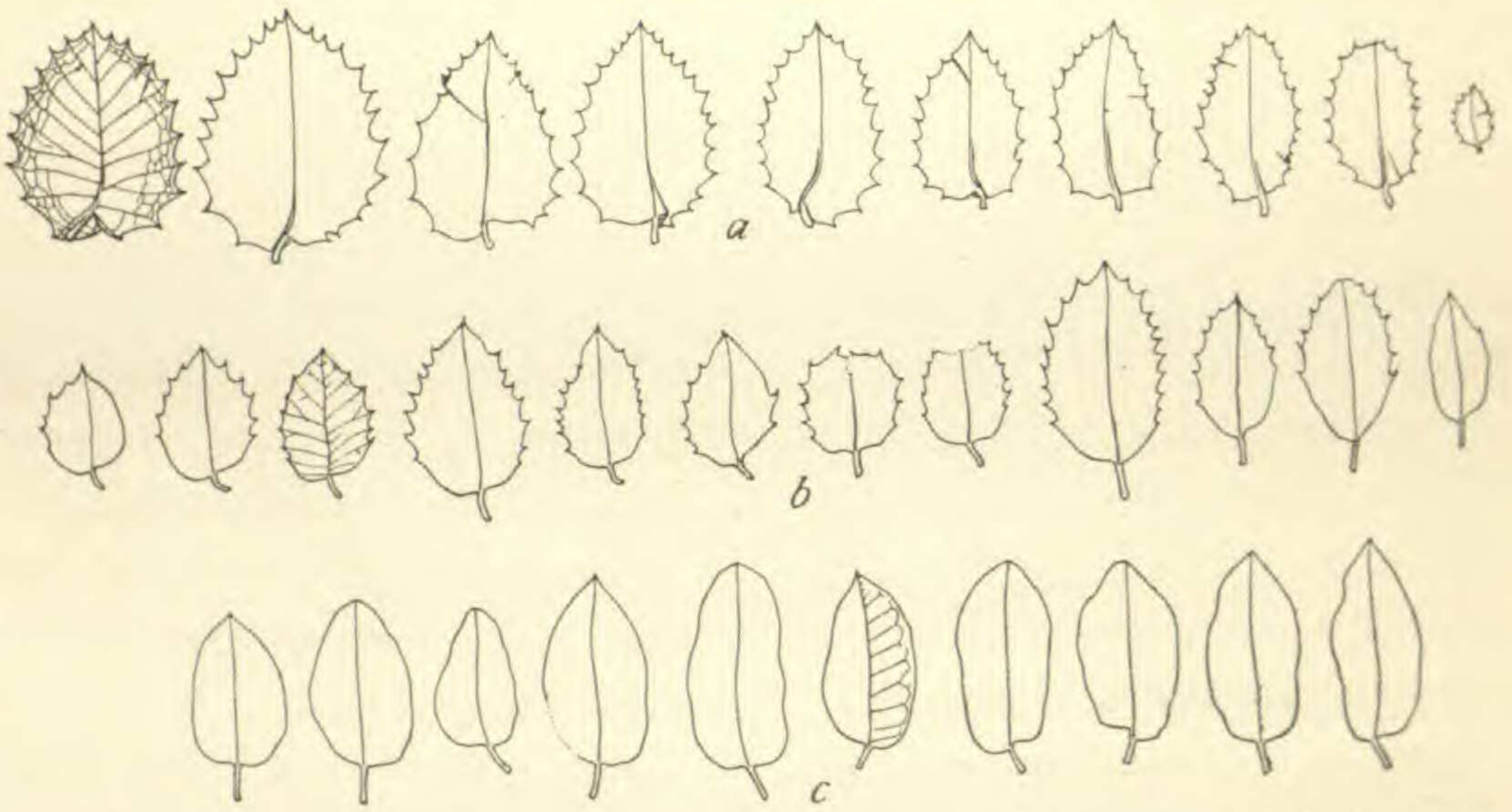

FIG. 1.—*Quercus chrysolepis: a*, alternate leaves on a branch; *b*, all the leaves on a twig; *c*, all the leaves on a twig. In all series from left to right is towards the apex.

at most a small and homogeneous group subject to a common impulse. We are in the habit of thinking of variations as concerning entire organisms.

More frequently, however, such leaf forms as these are not so strictly characteristic of whole trees; but single twigs show uniformly aberrant types of leaves; or most often single or few leaves of divergent forms are found scattered over the tree. *Fig. 2, a* represents the leaves of a single twig on which the leaf character changed profoundly during the season. This might have been ascribed to a change in the available water during the season, but that not all the twigs of the tree behaved in this way. *Fig. 2, b* shows the opposite change in the same season's growth, on another specimen from Chico; and *fig. 2, c*, representing four successive leaves on one twig of the same tree, shows how abruptly the size, as a character of the twig, may change. *Fig. 2, d* shows outlines of a number of leaves on one season's growth of a twig; in this case variation seems to have occurred not in the apical meristem giving rise to both axis and leaf, but in the primordia of the individual leaves.

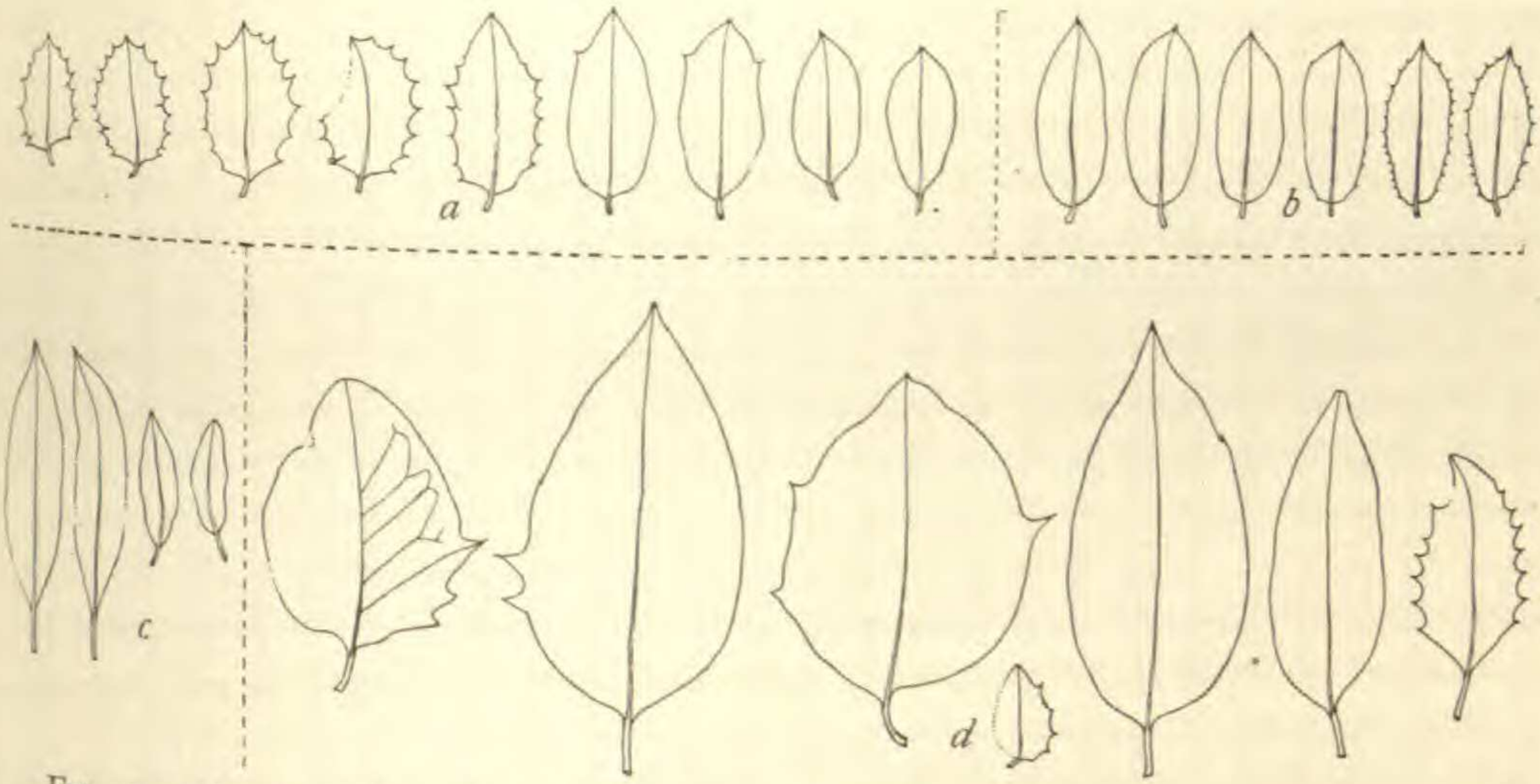

FIG. 2.—*Quercus chrysolepis: a*, all the leaves of a twig; *b*, younger leaves of a twig; *c*, consecutive leaves; *d*, some leaves on one season's growth of a twig.

QUERCUS DUMOSA Nuttall.

All of the figured leaves of *Q. dumosa* were collected in a single small patch of chaparral, on exposed parts of mature shrubs; their differences are therefore independent of the environment. *Fig. 3, a–b* are all the leaves of the last season's growth on two twigs of the same shrub, showing variation in the shape of the leaf as a character of the twig. *Fig. 3, c* shows single leaves from other parts of the same shrub, illustrating variation in single leaves. *Figs. 3, d, e* represent the characters of the shrubs as the varying entities; the shrub from which *fig. 3, d* was made bore conspicuously narrow leaves throughout, while *fig. 3, e* is from an example of the well-known bullate variety. This strain is so pronounced that it has been regarded as worthy of a distinct name; but it intergrades with the more typical form, and flat more or less spiny leaves are sometimes found on the same shrubs with the most bullate ones.

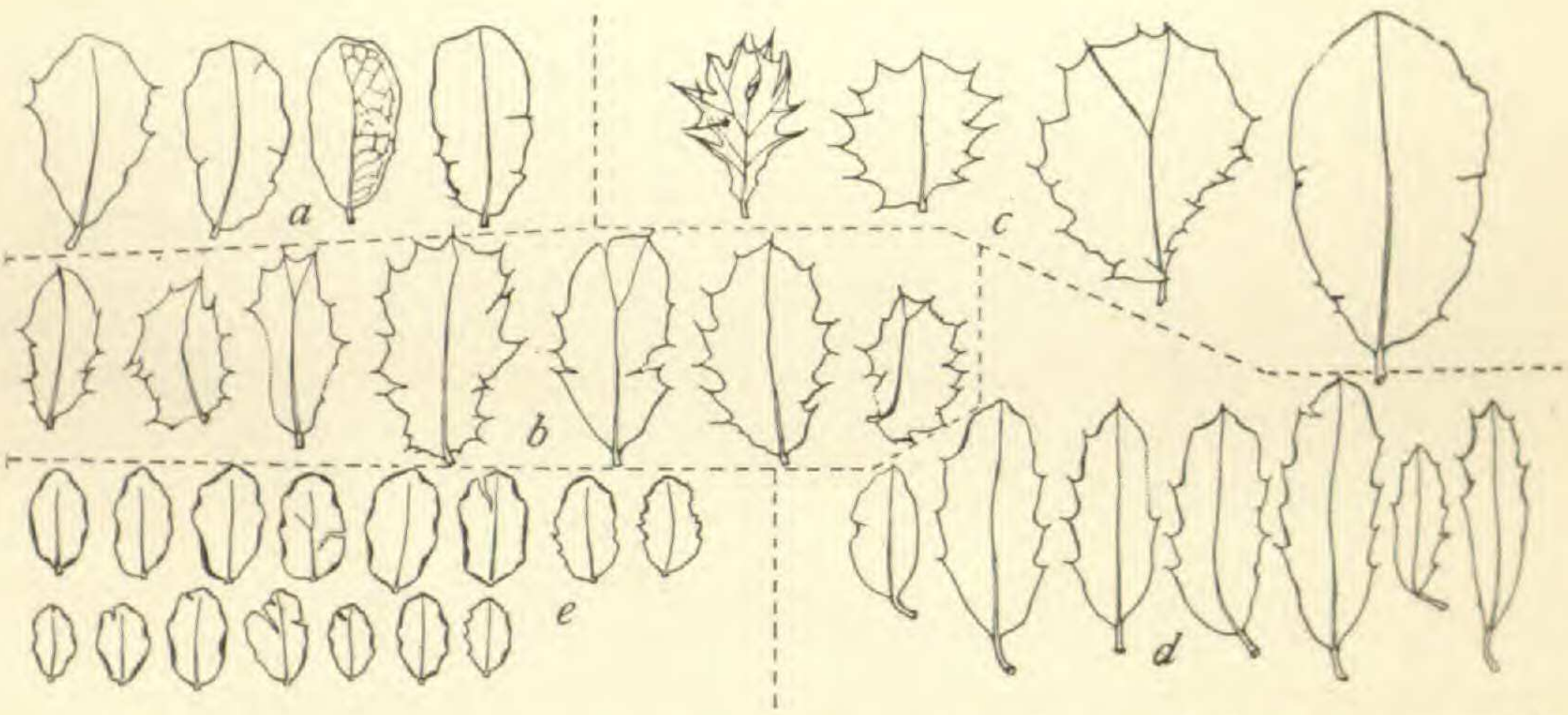

FIG. 3.—*Quercus dumosa: a,* all the leaves of a twig; *b,* all the leaves of a twig from same plant; *c,* single leaves from same plant; *d,* leaves of a twig of a bush with prevailing narrow leaves; *e,* leaves from the bullate variety.

QUERCUS WISLIZENI A. DC.

In the Santa Cruz peninsula *Q. Wislizeni* is a characteristic tree of the hilltops. In its typical situations it is less constantly and conspicuously variable in shape than the two species just considered. In protected spots it varies more noticeably, but as the influence of the environment may be directly expressed in these cases, they are left out of account. About Chico this is the common live oak of the valley, and is also common in the hills, and is as variable as *Q. chrysolepis* or *Q. dumosa* in that region. As in these, variation is by the tree, the branch or twig, or the single leaf. The difference between neighboring twigs on the same tree is illustrated by *fig. 4.*

QUERCUS AGRIFOLIA AND OTHER OAKS.

Q. agrifolia Née is the commonest live oak of the valley and lower hills about Palo Alto. It varies in the shape, size, thickness, and pubescence of the leaves, and like all the preceding may be entire or very much toothed. Variation is by the tree or any part of it, but is by no means so extreme and chronic as in the oaks I have illustrated; in other words it breeds truer to a type. The other live oak of this region, *Q. multiflora*, is quite restricted as to its habitat; its variation is inconsiderable. Among the deciduous oaks, *Q. Kelloggii* Newberry, which is common in the foothills and mountains, is most variable in its foliage (and fruit); decidedly more so than *Q. lobata* Née, the great white oak of the valleys. In the mountainous north end of the state, *Q. Kelloggii* is still very variable, as is the *Q. Garryana* Dougl., found with it. On the slopes of Mt. Eddy, *Q. vacciniifolia* Kellogg, ranging from the foot of the mountain up in an extreme case to well above "timber line," has as variable leaves as *Q. chrysolepis*. The leaves of the small oak of the moist wooded valleys of this region, known as *Q. multiflora*, are very uniform in all respects; but quite unlike those of the *Q. multiflora* of the south.

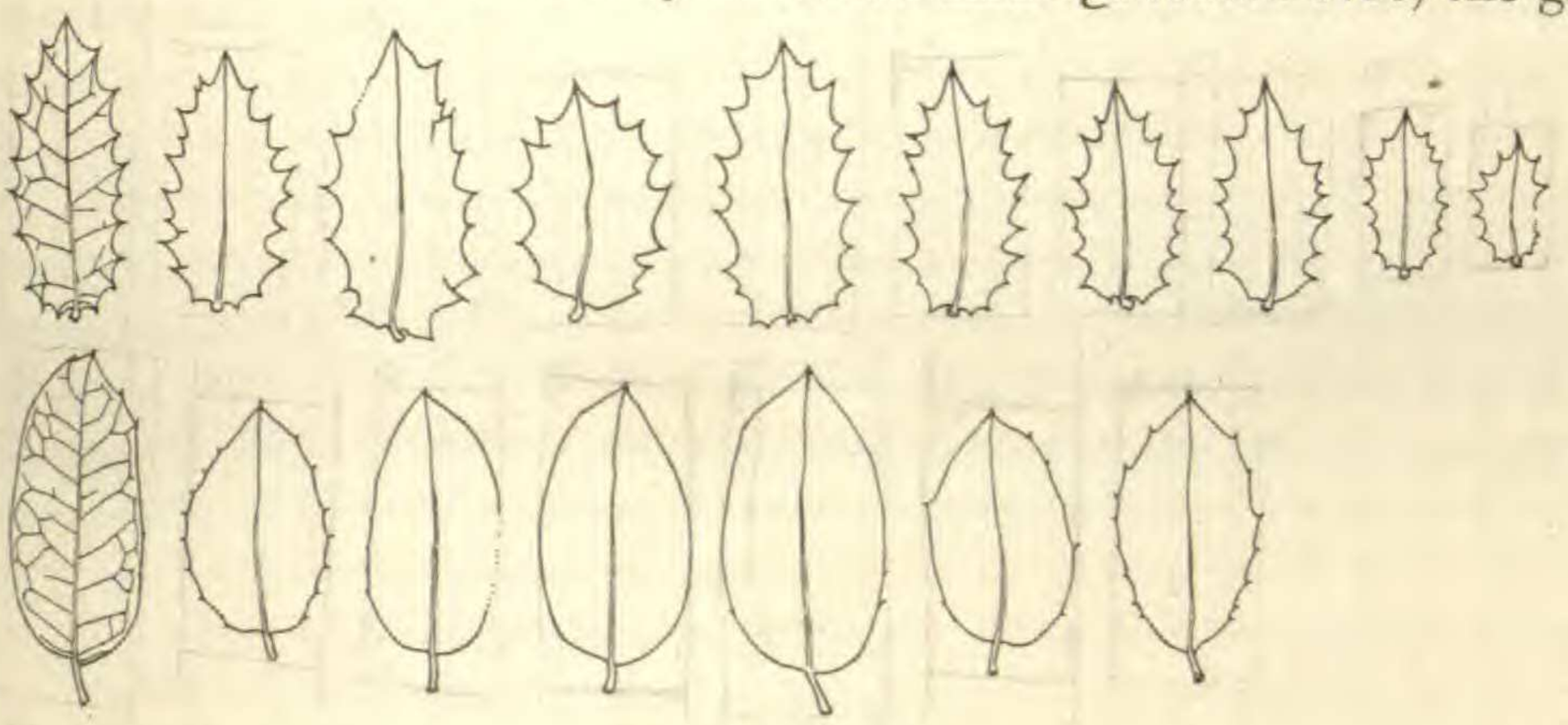

FIG. 4.—*Quercus Wislizeni:* all the leaves on two twigs of the same tree.

In the cases of all these oaks the fact cannot be too strongly emphasized that I have been discussing only real variation, as independent of any influence of the environment as experiment could have made it. The influence of differences of environment, wherever they exist, is very evident, and has been broadly handled by BRENNER.[1] He points out the great differences the environment causes

---

[1] BRENNER, W., Klima und Blatt bei der Gattung Quercus. Flora **90**:114–160. 1902; also Zur Entwickelungsgeschichte der Gattung Quercus, *idem* 466–470.

between the leaves of different trees, and even the leaves unequally exposed on the same tree; which naturally makes him skeptical of the value of determinations of extinct oaks by the remains of their leaves. The variations independent of the direct action of the environment, which I have just depicted, must strengthen the skepticism.

Before leaving the subject of Quercus I wish to discuss briefly BRENNER'S conclusions. He regards the less stability of the lobed forms of leaf as compared with the entire as evidence of the greater antiquity of the latter; such a difference in their *variability*—which should be a better test of newness than stability under varying environment—does not exist in this region. Still, considering oaks the world over, BRENNER may well be correct on this point. In his concluding paragraph, however, he exposes a classical weakness which needs pointing out as often as it occurs. It reads:

> Was als wichtigstes Ergebnis aus derartigen Untersuchungen hervorgehen dürfte, ist die so oft noch bezweifelte Thatsache, dass die durch äussere Medien hervorgerufenen Veränderungen an den Pflanzen thatsächlich erblich werden und im Lauf der Entwickelung zu eigentlichen Artmerkmalen sich entwickeln können. Durch den Nachweis, dass bei den Eichenblättern die Veränderungen beim Versuch und bei natürlichen Standortsunterschieden den mit dem Klima wechselnden Speziesverschiedenheiten entsprechen, hoffe ich einen Theil zur Kräftigung dieser Anschauung beigetragen zu haben.

If one accepts the inheritance of acquired characters *a priori* as "Thatsache," he may construe BRENNER'S observations as an illustration of it. But the direct reaction to the environment is fairly to be regarded as the result of natural selection, developed and preserved by virtue of its appropriateness; and since it is appropriate, it is obvious that by natural selection alone the plants varying in this direction spontaneously would be at an advantage, and in the long run would be parents of all the offspring. Since the identity of the forms assumed as a direct response to the environment with the forms characteristic of lands with the corresponding climate is fully explicable by natural selection alone, it is certainly no valid argument in favor of the inheritance of direct reactions to the environment.

My oak leaves will be discussed with those of the other woody plants.

RHAMNUS CALIFORNICA Esch.

In the foothills and mountains back of Palo Alto, *R. californica* and its var. *tomentella* Brewer and Watson are scattered promiscuously and merge by insensible gradations. The distinctions are supposed to be that the variety has tomentose reddish twigs, leaves yellow or white tomentose beneath, and peduncles longer than the petioles. My material was not collected at a season to illustrate the last feature. As to the others, individual shrubs possess or want them, so that a collector might easily gather material of the type or the variety; but in the field there is no constant relation between the color of the stem and the tomentum on the leaf, and neither green nor red twigs are likely to be glabrous. The leaves also vary notably in outline, apex, thickness, and margin, and in the rolling back of the sides. The most remarkable variability is in thickness and texture, margin, and pubescence. I have measured the length, breadth, and length of petiole of all the leaves on one twig (one year's growth) of twenty-eight bushes. In the following table the results, averages for each bush, are arranged according to the shape of the leaves, the ratio of breadth to length, because this ratio is a feature that can be exactly expressed, and one that could not possibly have been considered in the collecting. This ratio is of average width to average length, and is usually larger than the average of the ratios for the individual plants.

Further explanation of the table is as follows: under "margin" *s* is serrate, *ss* subserrate, *e* entire; under "lower surface" *g* is green and apparently glabrous, *wg* pale green and moderately pubescent, *w* white (sometimes yellow) and very pubescent; under "reflex" is given the per cent. of leaf folded back when pressed fresh; under "stem" *g* is green, *rg* reddish-green, *r* reddish, *rr* red; thickness is stated in units of a spherometer.

The length of the petiole is not significant. The width of the leaves is omitted from the table because expressed in the shape; it is less variable than the length, wherefore the average length of the relatively narrow leaves (55.7^{cm}) is greater than that of the rounder ones (47.3^{cm}). I did not attempt greater accuracy of description of the margin than calling it entire, subserrate, or serrate. This placed a majority of the leaves in the middle class, which includes leaves with a few prominent teeth irregularly scattered or only near the apex, or few or more numerous closely appressed teeth, or rarely

TABLE I.

Shape	Length in mm	Margin	Lower surface	Reflex	Stem Color	Leaf thickness
1.8	25.4	*ss*	*w*	9	*r*	139
1.9	62.9	*ss*	*g*	0	*r*	102
	27.8	*e*	*wg*	2	*rg*	106
2.0						
2.1	73.1	*s*	*g*	0	*g*	48
	51.1	*ss*	*wg*	2	*rg*	93
	34.0	*e*	*wg*	29	*rg*	122
	30.3	*ss*	*w*	34	*r*	164
2.2	48.5	*e*	*w*	36	*g*	182
2.3	70.8	*s*	*g*	0	*rr*	62
	62.8	*ss*	*wg*	3	*rg*	89
	50.1	*ss*	*g*	13	*rr*	148
2.4	47.0	*ss*	*g*	2	*rr*	102
	50.0	*ss*	*w*	1	*r*	127
	29.0	*ss*	*wg*	17	*r*	118
2.5	46.6	*s*	*g*	3	*rr*	100
	43.5	*e*	*g*	17	*r*	118
2.6	55.4	*ss*	*wg*	0	*rr*	178
	50.0	*e*	*wg*	40	*rr*	126
	38.7	*e*	*wg*	33	*r*	149
2.7	114.6*	*s*	*g*	0	*g*	58
	35.7	*e*	*w*	25	*rr*	196
2.8	61.5	*ss*	*wg*	6	*r*	181
2.9	61.7	*ss*	*wg*	0	*r*	92
	46.7	*ss*	*wg*	1	*rr*	132
3.0						
3.1	58.0	*ss*	*wg*	3	*r*	134
3.2						
3.3	43.7*	*e*	*w*	20	*r*	174
3.4	66.5	*ss*	*wg*	24	*r*	154

very numerous very minute teeth, so small as to give the appearance of none at all. Various parts of subserrate leaves may be entire. I could have counted teeth and reached a quantitative expression of the serrateness of some leaves, but the entire parts of leaves and the great difference in the teeth made such data rather meaningless. As the lower surface is described, the majority again of course occupies the broad middle ground, but there is no tendency toward any particular part of it.

These specimens were all collected in the vicinity of Woodside (a post-office a few miles from Palo Alto), which avoided the chance of extending the apparent range of variation by introducing geographical varieties. Selection of extremes in any direction was also avoided, by such devices as choosing a bush at too long range to more than recognize it.[2] Only the two starred in the table were collected after my attention was attracted to them by their many differences; they grew with interlacing branches in open ground by a roadside. No well-shaded bushes were chosen, nor shaded branches on the bush. While the immediate environment of the leaves was thus eliminated as a factor in making them different, the condition of the roots was left uncontrolled. I have no doubt that docking its roots would cause one of these shrubs to produce thicker, rounder, and more entire leaves, and I believe that these would tend to be pubescent beneath and rolled inward. But no visible differences in the ground were associated with the different variations. That the correlated variations are not common functions of any outside agent is evidenced too by their measure of independence—flat pubescent, entire green leaves, etc. The data in the table do not approach the range of variation of the individual leaves nor indicate the frequency with which the usually correlated variations are otherwise combined. The frequent correlation of thickness of leaf with pubescence, rolling backward, and evenness of margin might be due to such a combination of characters in heredity as many recent writers on inheritance assume; but I would rather ascribe it to mechanical factors which operate as the plant grows.

The range of the variability of this Rhamnus is not more remarkable than the absence of any well-defined type from which variation can be regarded as taking place; or, to express it in the usual way, in terms of curves, the curve representing any one of the varying characters under discussion would be conspicuously broad and low, without a well marked maximum and steep slopes. That this is true for the shape of the leaf the tabulated arrangement shows. If a curve were plotted with abscissae of 0.2, beginning with 1.7, the ordinates would be 1, 2, 5, 6, 5, 3, 2, 1, 2. If the length were plotted as a curve with abscissae of 1^{cm} (40 per cent. of the shortest leaf), the ordinates would be 3, 4, 6, 6, 5, 2, —1. If a curve were made to represent the thickness, with abscissae of 20 units of the spherometer (over 40 per cent. of the thinnest leaf), the ordinates would be 2,

---

[2] I have one branch of whose leaves the ratio of average length to average width is 4.25:1.00, but as I noticed its slender leaves before collecting it is not included in the table.

1, 3, 6, 6, 3, 3, 3; or if the abscissae represent 40 units, beginning with 40, the ordinates become 3, 9, 9, 6. The shape curves of variation of this plant must be clear from these three illustrations. Of course, the curve could be made steeper and narrower by increasing the value of the abscissal units; but by this process, if carried to an extreme, any curve can be reduced to a vertical line; and 40 per cent. of the shortest or thinnest leaf ought to be a large enough unit. The curves for the entireness of the margin and the pubescence of the lower surface would be of the same shape as these if there were scales by which they could be measured. These numbers are too few to make symmetrical curves, but as an objection to the validity of the conclusions this is largely removed by the fact that each number is an average of a considerable number of measurements.

ARCTOSTAPHYLOS TOMENTOSA Lindl.

This is the common manzanita of this region. Some authors have detected more than one species in what I include in it, but I am sure nobody would do so on my material. It was all collected in a limited region near the top of the mountain south of Woodside, using the same care to preclude the influence of local differences of environment as in collecting Rhamnus. Variable as it is, the manzanita has proved a much less favorable subject for this work than the Rhamnus, for several reasons. The most variable feature is the pubescence of both stems and leaves, and I have not found it feasible to measure this, because the chaff varies in size as well as in abundance, and is irregularly deciduous. Another difficulty is that the leaves formed at the ends of the seasons are smaller, narrower, and more entire than those typical of the plants; this made it necessary to discard some of the leaves, and to decide more or less arbitrarily where the typical leaves ceased on each axis. As this left too few leaves on each axis to furnish a safe average, I used all the fit leaves on the twigs of a small branch of each shrub. Tables II and III give the averages from thirteen plants, and the details of the individual leaves of one plant, to show their individual variability. The data under "margin" show the average number of teeth on each side of the leaf, and the average per cent. of the distance from base to apex at which the most apical tooth is found. Under base and apex their angles are given.

TABLE II.

Shape	Length	Margin		Base	Apex
		Teeth	Serrate %		
130	32.6mm	0.0	0.0	187.0	146.0
153	39.8	0.0	0.0	190.0	121.0
153	39.9	1.5	24.0	184.5	97.0
154	37.0	0.5	14.0	168.0	112.0
155	46.2	0.0	0.0	172.0	133.0
162	38.2	0.55	8.5	178.5	97.5
169	29.5	0.25	3.75	137.0	126.0
175	39.3	0.2	4.0	188.5	96.5
180	37.1	8.8	63.0	161.0	96.0
184	41.5	2.7	37.0	170.0	106.0
190	31.8	0.0	0.0	217.0	108.0
198	32.0	0.1	2.0	181.0	95.5
202	42.4	0.0	0.0	169.0	123.0

TABLE III.

Length	Width	Margin		Base	Apex
		Teeth	Serrate %		
49mm	27mm	4.0	50	175	90
46	25	2.0	25	165	120
43	28	4.0	80	195	120
46	24	5.0	30	165	90
47	23	1.0	15	165	95
47	28	3.0	30	195	120
30	19	13.0	85	150	90
45	23	0.5	10	165	130
39	21	1.0	30	180	115
41	22	3.0	50	150	90
48	25	2.0	55	150	90
40	21	2.0	30	170	75
31	18	0.0	0	155	120
42	23	2.0	20	150	105
40	21	1.0	20	180	100
43	22	4.0	45	160	100
42	24	3.0	60	165	120
35	17	0.5	10	135	135
34	19	0.0	0	165	120
46	23	1.0	25	165	120
41	20	2.0	25	150	95
38	22	5.0	60	180	100

BACCHARIS PILULARIS DC.

This is the most abundant shrub in the country about Palo Alto, growing practically everywhere. If *B. consanguinea* DC. is a distinct species, it does not grow here. The leaves (of *B. pilularis*) vary greatly from plant to plant, and also on the same plant. The size of the leaf varies on every plant with the order of the branch it is borne on; which made it so difficult to select a considerable number of leaves from different plants that as a whole should be fairly comparable that I did not try to make a table, but have preferred to reproduce the largest leaves from a few plants in a figure. *Fig. 5* shows the largest leaf of each of seven plants. Of two of these plants two leaves each are drawn, to show the difference in shape. Of these seven, the most exceptionally large leaf, on its own plant was the smallest of the lot, the most of the leaves on that plant being like those on the twig figured.

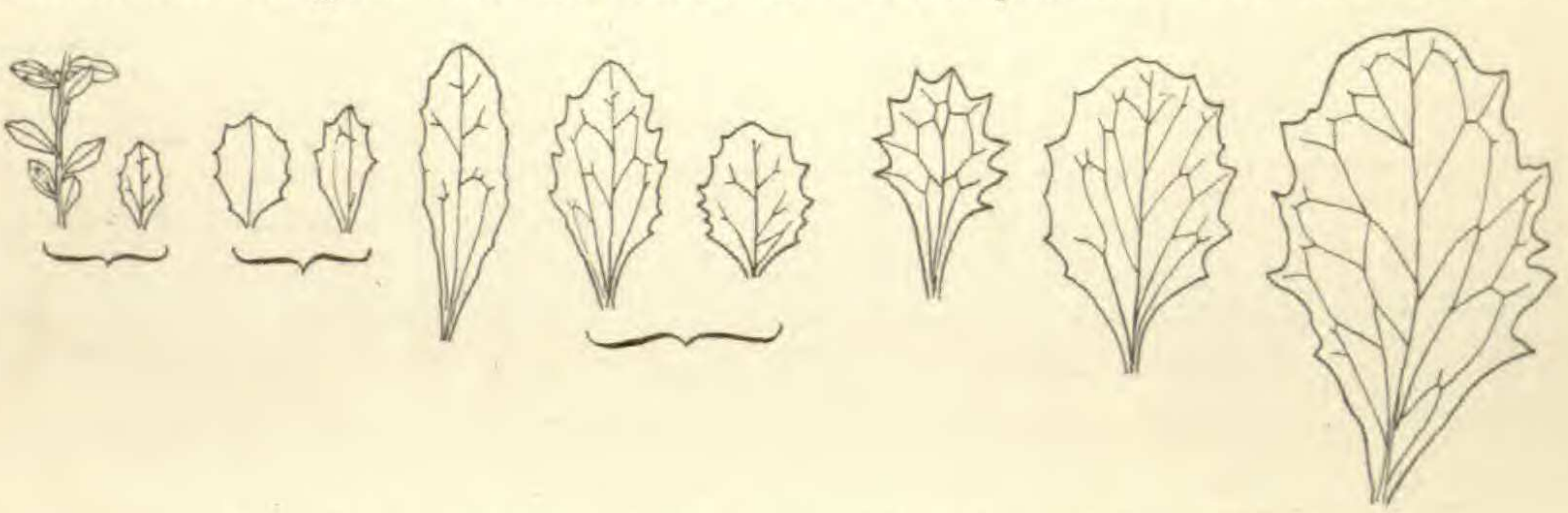

FIG. 5.—*Baccharis pilularis:* largest leaves of seven bushes.

CEANOTHUS SOREDIATUS H. & A.

The two commonest and most ubiquitous species of this genus about Palo Alto are *C. sorediatus* H. & A. and *C. cuneatus* Nutt. The latter is the common one of the valley and is rather the more variable, but I have not material to illustrate its variation in any one place. The plants of *C. sorediatus* from which *fig. 6, a* was made were collected in a small patch more than half-way up the mountain south of Woodside. Each leaf drawn was the largest on its branch. Beside the difference in size and shape, there is an uninterrupted variation, which my figure only suggests, from the dentate form, which I suppose gives the species its name, to one with quite entire leaves; and variation on the individual plants as well as between them.

Why are very variable plants common in this region? Because of the great local range in environments. There is a very strong probability that the offspring of a plant in the level east will grow under substantially the same conditions under which its parent grew, and that this will be true generation after generation. Under such conditions, variations fitting the plant in the slightest degree to its environment will in time be selected and will become specific characters. That even the most minor differences which serve as specific or even as varietal characters have the selection value this assumes I have not the least doubt; for they surely are not there to distinguish the species, nor for the sake of uniformity. It is heredity, acting within bounds established by the rigor of natural selection, that limits variation everywhere. In the mountains of the eastern states conditions are in most places hardly less uniform than in the great valleys; the seed may be carried as far as possible, but the seedlings will grow under conditions like those of their parents.

When one of these Californian shrubs or trees scatters its seed, there is a strong probability that the plants which grow from some of them will find themselves in surroundings decidedly different from those of their parents. Soils differ more in new and mountainous than in old and level countries. A difference of some 2000 feet in altitude, with a corresponding difference in temperature, is possible among the offspring of any one of these plants; and these are but minor differences in environment, the moisture and wind factors being the important ones. Some of the descendants of one of these plants may start to grow on high ridges swept by ocean gales; others on lower, only less windy, very dry and hot ridges and hilltops; others in the chaparral, dry and hot, but protected from wind; others in the fog-soaked passes, sheltered from most winds; and still others in the cañons, or rather gulches, deep and shady enough to keep the air fairly moist and still at all times.

If a plant grew in this region whose lack of variation enabled it to produce offspring uniformly well adapted to any one environment a large part of its seeds would be likely to fall where the seedlings must start to grow under conditions for which they were but ill suited; while a variable plant growing here has some chance that its offspring, wherever they find themselves, will be more or less at home. Since they all produce seed far in excess of what can grow, this means that in time the descendants of a variable plant will be found in considerable numbers under very different conditions; and that in this way it will be able to have many more descendants than the non-varying plant, the space available to whose offspring is limited. More descendants bear more seed, likewise variable, and with that they will thrive wherever they fall. And so the variable plant has some advantage in competition with the specialized one even where the latter is at home.

Where the environment is uniform over great areas, then natural selection breeds very close to a type, and considerable variation is a disadvantage; but where there are great and constant local differences in environment the premium is taken off of specialization, and natural selection favors a relatively high degree of variability. In such a place we find not merely that plants vary with the environment, but that in any single spot the individuals vary conspicuously as well.

If this is the real explanation of the variability of these plants, it is to be anticipated that plants of restricted range and characteristic habitat in this same locality will be more specifically adapted to their particular habitats, and when growing side by side with the ubiquists will be less variable. I have already pointed out that this is true among the oaks. The only other Rhamnus of this neighborhood, *R. crocea,* is not abundant enough even in spots to prove anything. In each of the other genera I have used, Arctostaphylos, Baccharis, and Ceanothus, we have other species of relatively local occurrence and relatively limited variability.

Baccharis viminea DC. is a plant of local occurrence on the flank of the mountains. Its leaves are sometimes entire, at other times sparsely serrate toward the apex; otherwise it is very constant. *Arctostaphylos Andersonii* Gray grows only near the mountain tops in the fog belt. The following measurements are of five plants selected in the field to show the extremes of variation; twenty-seven plants selected as were those of *A. tomentosa* would probably have varied less widely than these five do. No entire leaves were found.

Shape: 161, 169, 200, 203, 207
Length: 35.5, 44, 54, 46, 41.9
Serration %: 18, 76, 29, 36, 29

Ceanothus papillosus T. & G. is strictly confined to ridges in the fog belt, and is correspondingly constant. *C. thyrsiflorus* Esch. comes farther down the mountains, but not to their foot, and avoids exposed situations. The subjects of *fig. 6, b* were collected in the same place with those of *fig. 6, a,* at the same time and in the same way, before I realized that there was a difference in the variability of the two species, or suspected the reason for it. The contrast of the two is very striking.

II.

Some time ago I published a very brief note[3] on some freak ferns found in West Virginia, and suggested at the same time the interest of such freaks when the relation of minor and more conspicuous variations was being vigorously disputed. Since that time the mutation theory has lost none of its interest and probably none of its prestige. Meantime I have collected many more freak ferns, and some very full series illustrating less unusual variations; of these as many are presented here as seem necessary to justify the view that ordinary variations are indefinite in range and that extremes of series of such variations would be regarded as sports or mutations if found or collected alone. A detailed argument on this point with each fern shown would be superfluous. As in the former paper, I rely on figures rather than words to describe some of these ferns.

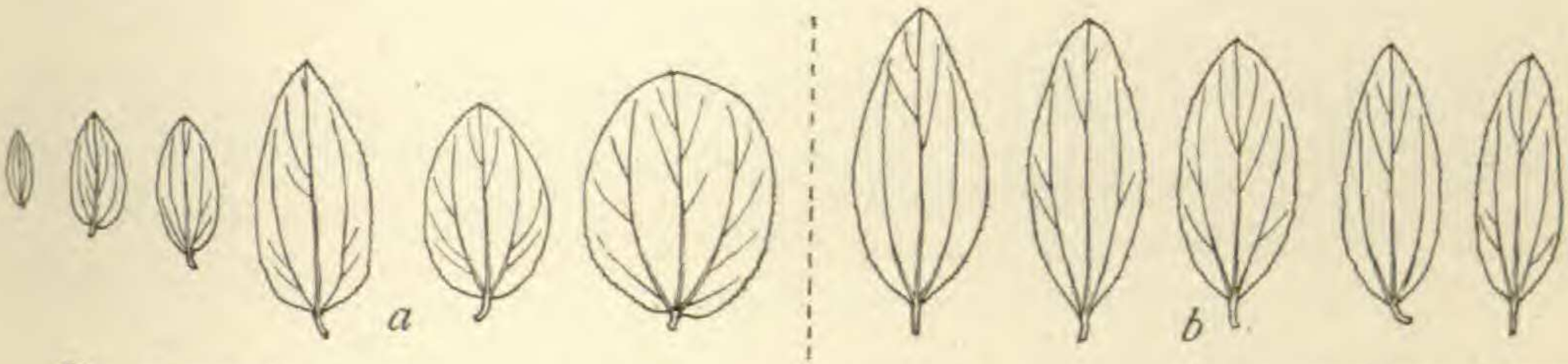

FIG. 6.—*a, Ceanothus sorediatus:* largest leaves of six shrubs. *b, C. thyrsiflorus:* largest leaves of five shrubs.

The variation in the extent to which some ferns are serrate, pinnatifid, or pinnate is very familiar. *Aspidium munitum* Kaulf. is usually only moderately serrate, like *fig. 7, b.* It varies in one direction to a form with teeth so closely appressed that at a distance it appears entire, and in the other to a form with compound teeth,

---

[3] BOT. GAZ. **34**: 142–144. 1902.

incised more than a third of the way to the midrib. *A. aculeatum* Swtz., in several varieties endowed with names, but freely merging, varies from a form but little deeper cleft than the most incised form of *A. munitum* to one in which these teeth become pinnae which in turn are cleft to the midrib into toothed divisions; that is, it varies from pinnate to tripinnate, the most divided part of fertile fronds being considered in every case. This variation could be duplicated in many ferns. It is doubtless continuous; but many of our fern species are founded on differences so small that a series of them would not bridge the gap between the extremes of this variation.

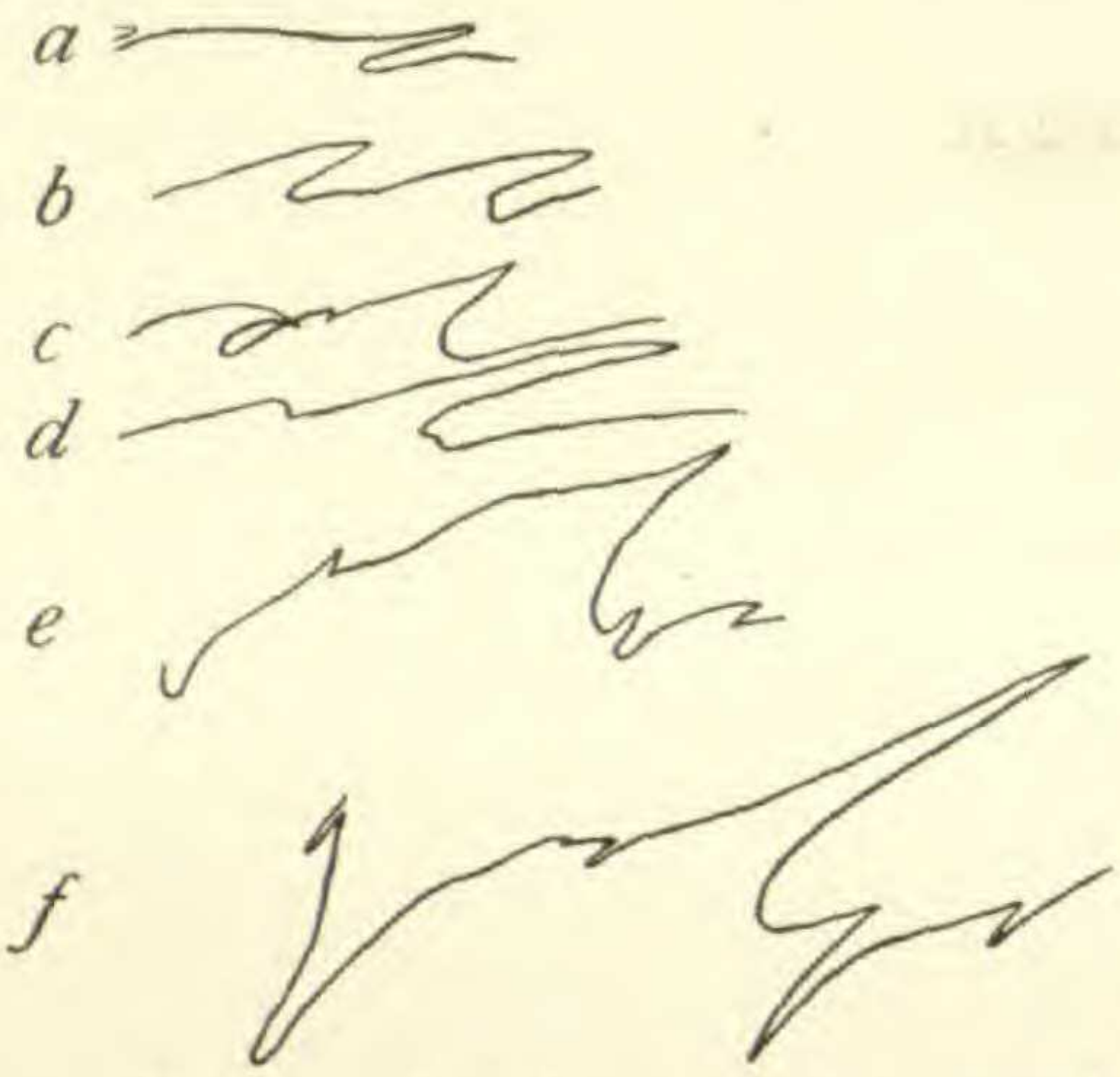

FIG. 7.—*Aspidium munitum:* teeth from six fronds, all drawn to same scale.

Fig. 8 is a fragment of a very abnormal frond of *A. argutum* Kaulf. Such freaks are not exceedingly rare. Some pinnae are usually normally developed, and there are all stages between these and mere lumps marking the place where pinnae should be. These freaks are almost always sterile, as other very abnormal ferns are likely to be. Reproduction is the consummation of normal development, and any deviation from the usual course is likely not to lead to this end. Of course, this is not true of ferns alone. I have found sterile freaks of a number of flowering plants among fertile normal forms. Reproduction demands a decidedly more perfect concatenation of favorable external and internal conditions than does growth.

FIG. 8.—*Aspidium argutum:* part of abnormal frond.

There are several different lines of interesting variation of *Polypodium californicum* Kaulf. One of these is the elongation of the pinnae, some or all of them, on a frond. Fronds noticeably more acute than the normal are not rare, but of course the more extreme variations are proportionately seldom found. I have some twice as long as the normal; but none so conspicuous in this respect as the *P. vulgare* from West Virginia, in my other note on this subject. Another line is the increase in the size of the teeth and the deepening of the incisions between them until the pinna is pinnatifid, even to the midrib on the lower side. In this case the number of times the veins are forked is greatly increased, which disturbs one character often deemed specific in Polypodium; and the veins all remain free, which would be more notable if the separation of Goniophlebium as a distinct genus were natural. In merely serrate plants the union of the veins to form areolae of the Goniophlebium type may or may not occur, the anastomosis or its failure being utterly without rule, even on single fronds or single pinnae.

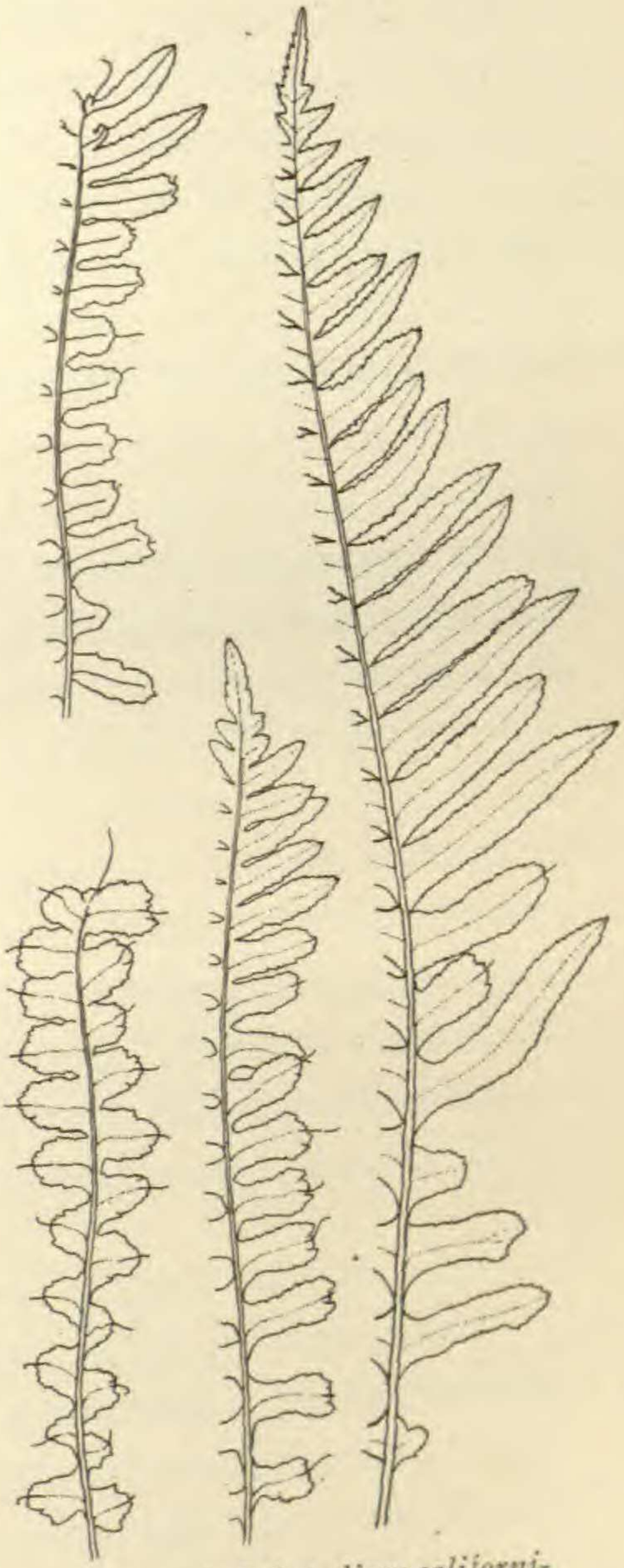

FIG. 9.—*Polypodium californicum:* a series of abnormal fronds.

The anastomosis is likewise irregular in the fern known as *P. Scouleri* Hook. & Grev., which is so unstable in other respects that it would as well be considered a form of *P. californicum*. Down close to the beach, where the typical form of *P. Scouleri* is found, it is variable, there being from three to twelve pairs of pinnae, which are "typically" twisted and thrown forward until they all fold in pressing, but are sometimes perfectly plane. Where more protected they are thinner, with more acute pinnae. To what extent *P. Scouleri* represents the direct action of the environment, and to what extent it has developed into a really independent species can only be determined finally by experiment, but certainly it is very variable, and is also profoundly modified by the environment. Its variability is evidence on the point demonstrated by the oaks and shrubs.

A most remarkable monstrosity, many individuals of which have lost all characteristics of *P. californicum* and are indistinguishable from a freak of *P. vulgare* reported from Germany, was first found near Chico, where it had complete possession of a small patch of ground (*fig. 9*). Its essential feature is that the distal part of the midrib of the lateral pinnae and segments, and the whole axis of the terminal one, develop no wing, but spring free from the spore-bearing surface of the blade. In correlation with this, the growth of the segments is arrested, making their apices round and dentate, and the frond as a whole truncate-oblanceolate. The free part of the midrib may be prolonged to at least the natural length of the segment; or may be shorter, even to the extent of not springing free at all; in which case the development of the blade may be anywhere from very stunted to normal. All the pinnae may be affected; or some of them toward the apex may not; or only a few or a single one may be modified, making a complete series from normal fronds to the most monstrous. Since collecting it near Chico, I have twice found a few ferns like these back of Palo Alto, but in these only a part of the segments were ever malformed.

III.

I wish now to use this material, both the shrubs and the ferns, as the basis for a discussion of the "mutation theory" in bionomics. It is already clear enough that I do not believe there is any foundation at all for the view that mutations as essentially distinct from ordinary variations exist. That they do not I endeavor to show. But the mutation theory under one or another caption has for years been a refuge for those who on any ground regarded natural selection as inadequate to the demands upon it, and has recently been so powerfully supported by DE VRIES and others (BATESON, WETTSTEIN, etc.), and has been so enthusiastically received that it has become a proper subject for discussion by those who recognize no ground for it.

The mutation theory does not, as some of its supporters seem to believe, do away with the doctrine of natural selection. This doctrine is that among more living things than can live and bear progeny those best adapted to the existing environment will survive. It assumes, what is the fact, that the existing organisms differ. The mutation theory would explain the origin of the differences, saying that from their first appearance they are too wide and fundamental to fall in the category of "individual variations." The more prevalent idea since DARWIN has been that these minor, incessantly appearing differences were the raw material for nature to select among, and that by the constant survival of the individuals with the slightest advantages new races, varieties, and species might arise; but every partisan of natural selection recognizes variation as prerequisite to any evolution. The apparent issue is: "are the differences whose perpetuation gives rise to new species the ordinary individual variations, or the less usual but more considerable mutations?" But a question which should obviously be settled first is: "are individual variations and mutations distinct?"

Since I do not believe that the differences between the offspring of common parents differ fundamentally among themselves, it is but natural that I should be unable to frame a definition of a mutation which would really distinguish it from the general run of variations. For the most authoritative definition I have consulted DE VRIES'S *Mutationstheorie*. To my surprise, I have read the book, and then very carefully re-read the general part, without finding anywhere anything that has the force or form of a definition.

In the introduction, where "es sich darum handelt, den Unterschied der beiden Grundformen der Variabilität so klar wie möglich darzuthun," he says: "Die Mutationen sind Vorgänge, über deren Natur wir noch sehr wenig wissen. Die bekanntesten Beispielen solcher Mutationen sind die sogenannten spontanen Abänderungen ('single variations'), durch welche scharf unterschiedene neue Varietäten entstehen. Man nennt sie auch wohl Sprungvariationen" (p. 4). Again he says (p. 22): "Die letzteren [single variations] sind zufällige, spontane Abänderungen, unseren Mutationen *entsprechend*" (italics mine). And (p. 23): "Die *single variations* sind zufällige, nur von Zeit zu Zeit auftretende, sprungweise die Formen verändernde Erscheinungen." He says (p. 5): "Die Gesetze der Mutabilität sind ganz andere als jene der Variabilität;" but this clue to the distinction fades when we read (p. 23) that "Die 'single variations' sind zufällige Erscheinungen, von deren Gesetzen man bis jetzt keine Erfahrung hat."

Calling single variations and saltatory variations and discontinuous variations synonymous with mutations does not tell what any of them are. The one criterion by which DE VRIES tries consistently to distinguish mutations is their giving rise to specific characteristics. This certainly does not admit of practical application, because we do not know how to identify a specific characteristic. It is a very tenable position at present that the species is a group of organisms with limits set by our convenience, and that many "valid" species—to put it moderately—are characterized by distinctions which are matters of degree. The specific characteristic can hardly be more clear-cut than the species it characterizes. If specific characteristics are in nature unstable and not exactly definable, this one means of identifying mutations is imaginary, in addition to being inapplicable. DE VRIES holds that species, not necessarily with the usually recognized limits, are definable and never have merged, and that their individual characteristics are likewise definable and stable; but when he identifies these in turn by their origin by mutation, he brings his argument into a circle.

The practical characteristic of mutations on which DE VRIES lays most emphasis is their inheritance: "Solche sind fast stets entweder völlig oder doch in hohem Grade erblich" (p. 16). But, as he of course recognizes, the continuous individual variations are also hereditary. We see that on every hand. The most familiar examples are furnished by human beings. DE VRIES says explicitly that the differences between them have not arisen by mutation as he uses the term. Yet what characteristic of any species is more certain to be inherited than the straight hair or the black hair of a pure Chinese, or the complexion of an Ethiopian or an American Indian? Among the much less constant features of our own race we know how likely the color of the eyes and hair, and other physical peculiarities, and even mental eccentricities, are to be inherited. On the other hand, mutations are not always inherited, as DE VRIES'S observations on Oenothera show; and if they were, there could be no mutations. Variations certainly differ in the reliability with which they are inherited; but mutations, if there were such, would not be distinguishable from other variations in this respect, unless sometimes in degree.

Many authors have sought to distinguish single variations or discontinuous variations from the continuous individual variations by the extent of the deviation from the parental type. DE VRIES does not lay himself liable on this point, saying explicitly that they are not distinguishable in this way (p. 41): "Die Betrachtung mancher *single variations* hat die Einsicht eingebürgert, dass die Mutationen jedesmal bedeutende Veränderungen sein müssen, namentlich, dass sie grösser sein sollten als die Variationen. Solches ist aber durchaus nicht der Fall, und anscheinend sind wenigstens zahlreiche Mutationen kleiner als die Unterscheide zwischen extremen Varianten."

If mutations cannot be recognized by their range of deviation, nor by their being inherited, from other variations which may chance to be unusually wide and to be hereditary, there is no test by which they can be recognized. If a practical definition of a mutation had ever been framed, it could not have escaped DE VRIES; and if his idea could be formulated so that it would represent a distinct phenomenon recognizable as such in nature, he would certainly have given it that form. I agree heartily with its friends in welcoming DE VRIES'S work as the most valuable empirical contribution to our knowledge of the origin of novel forms of organisms since the *Origin of Species;* and that DE VRIES'S method—the analysis of the composite character of a species into its elements, and the study of the origin (*and change*) of these—is far more rational and promising than the study of the "species," as we recognize them, as a whole. But I regard his mutations as generically different from ordinary variations, and his specific characteristics as distinct and clear-cut in their existence and abrupt in origin, as undefined and not scientifically definable, because not representing distinct natural phenomena.

DE VRIES'S recognition that the discontinuity of "discontinuous" variations does not necessarily distinguish them from "continuous" variations is one of the best evidences of his familiarity with the subject. Numerous writers ascribing to discontinuous variations the same importance he does to mutations have, as he says, regarded them as fundamentally distinct in the range of their deviation. Some of these writers have regarded their importance as a function of the extent to which they are aberrant. This question has been threshed over so thoroughly that I do not care to touch on it more than to suggest again the frequent sterility of sports. The assumed distinctness of discontinuous variations is, however, by no means so trite a subject.

I disbelieve in the distinctness of these two classes of variations on empirical ground, and *a priori*. We will consider the former first. If they are distinct, it must be possible to draw a line between them, and to say positively of any variation with which we are thoroughly familiar that it is the one or the other, and to give a reason for the judgment. It will be classed as discontinuous only when the series of less considerable variations in the same direction breaks short of it. But every first-hand worker in this field knows that such series always tend to fill when the material is increased. In variation within wide limits or limits approximately but not absolutely fixed, the extremes of any finite number of examples are likely to be disconnected. When the number is increased sufficiently the gaps fill up, but new isolated extremes are found. Do the variations which are assimilated to the regular curve in this way thereby become continuous? If "discontinuous" means anything, they do; and if they do, it obviously does not mean very much.

My abnormal ferns illustrate this assimilation of apparent monstrosities into a regular series with the accumulation of enough material. The Polypodium I described from West Virginia, with the apical segment and its neighbors greatly enlarged, seemed most remarkable when I first collected it; but a thorough search of the spot the next season showed a long series of specimens bridging the gap between these seeming monstrosities and typical plants. I have had the same experience with several lines of variation of *P. californicum*. In its extreme form the caudate monstrosity, with the frond as a whole narrowly oblanceolate, the individual segments abnormally broad and widening toward the round or retuse apex, and the midrib springing as a long curved hair from the dorsal surface, is the most extreme freak fern I have ever seen. From its occurrence in compact patches I am sure it is as near as nature comes to a mutation in DE VRIES's sense. And yet, examining hundreds of specimens, I have found a very complete series of steps connecting it with typical plants. Does the fact that thorough search fills the series class this freak outside of discontinuous variations,where it would unhesitatingly be placed if I had done less hunting? What fern in the series is just aberrant enough so that if found alone it would constitute a mutation? An answer should be possible if mutations and variations are distinct.

Polypodium californicum with its veins all free exhibits variation not merely beyond the limits of the species, but beyond those of the subgenus.[4] That would be a mutation surely; but I have fronds of this kind and others with some anastomosing veins from the same rhizome; fronds with anastomosing veins on one side of the rachis and free on the other; and fronds with the two forms of venation variously distributed among the segments. Among the fungi I have a number of examples of extra-generic variations, as the genera are now limited; but the boundaries are so artificial or dubious that most of these have no certain interest at present. In a dozen or so American species of Puccinia, spores of the Uromyces type are common or at least known. In collections of Lenzites from a single log, I have specimens with many connected lamellae, and others with all of them free, which by themselves would unhesitatingly be referred to Agaricaceae, and still others strongly suggestive of Irpex.

It is hardly worth while to rehearse more instances in which mutations and ordinary variations cannot be distinguished; these few seem to me to prove the case as well as more would do it. If mutations and variations were fundamentally different, it would be possible to say of any one of these peculiar ferns that it belongs in one or the other category, and the more copious the material the easier it would be to apply the classification; if it were but natural. But the more thoroughly I have collected and examined them, the more evident it has become that the slight and extreme variations differ only in degree. I am quite aware that this evidence is not of the same kind as DE VRIES's, and that his has a value in the study of heredity which mine absolutely lacks.

---

[4] Goniophlebium was regarded as a distinct genus by BLUME, and is just now restored to that rank by UNDERWOOD.

My evidence is appropriate, however, to the question at issue. Irrespective of the individual parentage of the plants, it shows that the distinction between wide and narrow, or continuous and discontinuous, variations is artificial. That these aberrant forms should be the result of several generations tending in the same direction would be incomprehensible in view of the sterility of some of the forms and partial sterility of others; and would itself be contradictory to DE VRIES's idea that new forms of plants arise suddenly, without preparation or intermediate steps.

The *a priori* objection to really discontinuous variation is the impossibility of really discontinuous development. Every organism that varies grows, and varies only as it grows. All organisms of any kind are indistinguishable during a considerable part of their development, but sooner or later their individual differences appear and become fixed. The tendency of heredity, as the conservative factor in both evolution and development, we believe is to postpone the appearance of deviations from the parent types. If they appear very late, the variations will be very small; if they appear earlier, they will obviously be more notable. If variations in growth appear much earlier than usual, the variation will be unusually profound. But it must be evident to anybody that it is not possible to select any point within the range of known deviation in the development of any organism whatever, and to say that the differences which occur before this time are different in kind from those which appear at and subsequent to it.

Variation, when it is just appearing, is a phenomenon involving small and homogeneous groups of cells; or, regarded in finer detail, single cells. When variation occurs it is by the unit of the varying structure. If it occurs early, the subsequent development of the units can make it become very conspicuous; but the variation *is* when it *is*, irrespective of later growth based on it. Stomata and trichomes are as a rule formed late in development, and the presence of two where one is normal is likely to escape our attention, as is the presence of an extra leaf on a tree; cotyledons are formed earlier, and an extra cotyledon, perhaps involving an unusual form of the whole plant that grows from the seedling, is an object of interest and remark. But when the first step toward the formation of the extra cotyledon was taken it was certainly as small as can be imagined. And surely there is no point between the formation of an extra cotyledon and that of an added leaf on a season's growth where mutations leave off and variations begin. Both begin with the formation of two growing points from one. Every step in growth is an insensible move from the preceding state; and variation, inexorably dependent on growth for its appearance, cannot be less continuous than growth is.

It may be objected to this argument that the variation does not occur in growth, but before it begins; say in the formation of the germ cells. That cannot be demonstrated, even in as favorable subjects as the insects. And if it were really and demonstrably true, it would not damage the argument, but merely shift it. Life is an uninterrupted process from generation to generation. The division of the chromosomes, the reduction in their number, and their combination in the sexual union are orderly, regular processes, just as the growth of any individual is. In our ignorance of the forces at work and their way of working I can imagine no discontinuity in these finer, more recondite processes, any more than in more visible growth. Nor can I see why we should regard differences between twin organisms as not arising in growth because we suppose their environment to be identical, and on that ground refer the differences which we certainly do see to still earlier stages in ontogeny, perhaps even antedating fertilization; unless we can show differences in the environment there. It is perhaps natural to suppose that the things we do not understand happen in the stages we know least about, but this assumption does not share the nature of a proof. It is therefore sophistry to plead that variations are independent of growth as an objection to the principle that they must be as continuous as growth is.

If variation is a phenomenon of growth, it may occur wherever growth is going on. In the beginning of this paper I have pointed out that it actually does this in the oaks I studied. It is as reasonable to speak of variation localized in the parts of a tree, each the product of the activity of an isolated meristem, as to regard the differences between parthenogenetically produced offspring of a single parent as examples of it. KELLOGG has shown that variation is more considerable among the parthenogenetically than the bisexually produced members of a hive of bees.

SUMMARY.

In this part of California, where conditions are locally very diverse, plants are more variable congenitally than in regions where the environment is uniform. For in the latter, natural selection acts along the same line on many generations, and the more closely plants breed true to forms fitted to their uniform environment, the better are their chances of perpetuation; while here natural selection is unlikely to work in the same way on many generations of variable plants; and breeding very close to a form fitted to any one sort of environment decreases the number of the plant's prospective descendants.

For the same reason, the ubiquists in this region are more variable than the plants of restricted occurrence. Their variation enables them to be ubiquists, and being ubiquists keeps them variable.

"Mutations," or discontinuous variations, and the most insignificant of individual variations are parts of one unbroken series.

Government Laboratory,
Manila, P. I.